Oribatid Mites and Nutrient Cycling

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INTRODUCTION

Communities of oribatid mites (Cryptostigmata) in leaf litter and forest soils consist of an impressive number of individuals. Total populations of the order of 10^5 oribatids per square meter are commonly reported from forest floors. Because of their numbers, oribatids have been believed to be important contributors to the breakdown of organic detritus. Since the pioneering work of Bornebush (1930), attempts have been made to evaluate the energetics of oribatid mite populations, often leading to the conclusion that a small fraction of the energy flow of decomposition passes through oribatids. Recently new emphasis has been placed upon the indirect effects of consumers as regulators for ecosystem processes (Chew 1974). Indirect effects may be more appropriate than energy flow for evaluating the functional role of oribatids in decomposition systems. Various indirect effects have been proposed for oribatids: fragmentation of litter, inoculation with microbial spores, stimulation of microflora by grazing, and so forth. Some experimental evidence supports these suggestions (Van der Drift and Witkamp, 1960; Madge, 1965; Witkamp and Crossley, 1966) but quantification of the importance of such indirect effects is difficult to obtain.

Mineral or nutrient element cycling has emerged during the past decade to rival energy flow as a means of quantifying ecosystem processes (Waide, Krebs, Clarkson, and Setzler, 1974). Studies of mineral cycling possess several advantages over energetics. The phenomenon of cycling allows for the study of feedback loops among ecosystem processes, whereas energy flow is unidirectional. Evaluation of feedback loops can be a means of quantifying indirect effects of consumers. The availability of radioactibe isotopes or radioactive analogs of mineral elements allows for the direct measurement of transfer rates. In decomposition studies applications of radioactive tracers have helped to identify pathways of transfer from microflora to oribatids (Coleman, 1970).

Indirect effects of microfauna on mineral cycling were demonstrated by Witkamp and Crossley (1966). Reduction of arthropod populations with napthalene was shown to have a more drastic effect upon radiocesium (an analog of potassium) loss from decomposing litter, than upon weight loss. New analytical techniques may enable studies of elemental movement on a smaller scale than was previously possible. Energy dispersion X-ray analysis (Russ, 1971) has the potential for measuring nutrient and mineral element concentrations in oribatids and associated microflora (Todd, Cromack, and Stormer, 1973). Applications of such techniques may elucidate complex relationships between soil microarthropods and microflora, which may be influencing or regulating elemental release during decomposition.

Only a few studies thus far have measured mineral or nutrient concentrations, accumulation or turnover by oribatid mites. Kowal (1969) measured calcium-45 accumulation by Cultrotibula juncta, thereby estimating rates of feeding on natural pine mor. Kowal and Crossley (1971) estimated ingestion for "immature oribatei" and "mature oribatei" in pine mor microcosms, using uptake of calcium-45 for rate measurements. McBrayer and Reichle (1971) performed a similar experiment using ^{137}Cs, an analog of K. Luxton (1972) measured ^{32}P assimilation and excretion by nymphal and adult Damaeus clavipes, as a means of calculating energy intake and assimilation. Gist and Crossley (1975a, 1975b) reported turnover rates of elemental contents for mineral elements in Cryptostigmata. Gist and Crossley (1975c) included oribatids in a model estimating mineral element fluxes in forest floor of a southeastern hardwood forest. Todd, Cromack and Stormer (1973) and Todd, Crossley and Stormer (1975) measured mineral element content of oribatid mites using an electron microprobe technique.

Advantages of nutrient cycling studies with oribatid mites fall into two general categories. First, these studies yield an estimate of the direct participation of oribatids in the process of litter breakdown, with resultant nutrient release. Secondly, the utility of feedback loops in nutrient models may provide a means for evaluating indirect effects of oribatids in the general decomposition phenomenon.

INPUT - OUTPUT MODELS

A common conceptual model of nutrient accumulation by arthropods such as oribatids is based on the balance between intake and loss of nutrients:

$$\text{Accumulation} = \Sigma(\text{intakes}) - \Sigma(\text{losses}).$$

Intakes occur as ingestion from one or more food sources. A variety of nutrient losses occur. Nonassimilated nutrients may pass rapidly through the gut, a problem discussed below. Assimilated nutrients may be lost by excretion or biological turnover. Secretions, losses of body parts, or losses of exoskeletal material during molting, are other sources of nutrient loss. At the population level mortality is a loss from the nutrient pool. Migrations also may affect pool size. Many of these rates may be time-dependent, in that they may vary seasonally. Even within season, rates are doubtless temperature and moisture dependent as well. Furthermore, rates may be expected to differ for each species of oribatid, and for life history stages within species.

The implementation of a precise nutrient accumulation model would require a great deal of detailed information about each oribatid species. Such information will doubtless remain unavailable for some time to come. An obvious alternative is to simplify the conceptual model with generalizations of rates and parameters. Such generalizations can be valuable if they provide hypotheses which are subject to experimental proof or falsification. Existing hypotheses are so general that experimental validation is possible only at crude levels (Chew, 1974).

A simplified model for nutrient accumulation by Cryptozoa (including oribatids) was recently described by Gist and Crossley (1975b). Nutrient content was assumed to be in dynamic equilibrium. Nutrient intake was separated into assimilated and nonassimilated proportions. Turnover rates were separated into defecation of nonassimilated nutrients and excretion of assimilated nutrients. The model was represented as:

$$\frac{dX_t}{dt} = Ip_1 - \lambda_1 X_1 + Ip_2 - \lambda_2 X_2$$

where: X_t = nutrient element content in the total organism
X_1 = nutrient element content in the gut
X_2 = nutrient element content in the body tissues
I = rate of ingestion
p_1 = nonassimilated fraction of ingestion
p_2 = assimilated fraction of ingestion
λ_1 = gut loss rate
λ_2 = body tissue loss rate

By assuming that nutrient concentration in the body does not change with time ($dX_t/dt = 0$) it was possible to estimate nutrient intake. Assimilation proportion and turnover rates were measured with radioactive analogs of K and Ca. The results were utilized in a systems model of nutrient dynamics in a food web of a hardwood forest floor (Gist and Crossley 1975c). Results from this model, and those for an adjacent white pine watershed (Cornaby, Gist and Crossley 1975), suggest that the cryptozoan fauna ingests a significant proportion of the annual input of Ca and K to forest floors. Oribatids were found to be among the dominant cryptozoan groups processing nutrients.

PARAMETERS FOR A GENERALIZED INPUT - OUTPUT MODEL FOR ORIBATIDS

To evaluate the direct versus indirect effects of oribatids on nutrient cycling, additional and better information will be needed. Estimations for rates of direct ingestion, assimilation and excretion of nutrients are based on few measurements and possibly uncertain assumptions. New analytical methods and radiotracer techniques are currently improving this base of information. These developments are reviewed here, emphasizing the two mineral nutrients K and Ca.

Elemental content of oribatids. Little information has been developed on nutrient element content of oribatids. Tedious separation is required to obtain the thousands of individuals needed for AA spectrometric analysis. Results reported by Gist and Crossley (1975c) and Cornaby (1973) showed that oribatids had unusually high concentrations of Ca (35,000 to 60,000 ppm). Wallwork (1971) found that oribatids generally have high ash content, and reported "large deposits of $CaCO_3$" in the cuticle of Steganacarus magnus.

A recent innovation is the use of electron microprobe analysis for measurement of mineral element concentrations in small biota such as oribatids (Todd, Crossley and Stormer 1974). With this technique it is feasable to measure concentrations of some elements in individual mites or even parts of mites. Current research is utilizing energy dispersion X-ray analysis in conjunction with a scanning electron microscope (Russ 1971) for these measurements. Results (Table 1) confirm high concentrations of Ca in oribatids generally. Concentrations of Ca in Mesostigmata and Prostigmata are lower than might be anticipated. Concentrations of K obtained by this method are lower than the range of 5,000 to 12,000 ppm reported by Gist and Crossley (1975_a_) for cryptozoans generally. Problems may exist in the proper standardization of microprobe techniques for these arthropods.* Even so, the results confirm high Ca contents in oribatids, and reveal considerable differences between species. It would appear that Ca concentration is not necessarily related to rugose or thickened integument. Highest values are reported for _Liacarus_, an oribatid with a smooth integument. _Camisia_, with a rugose integument, has low values. Concentrations of Ca also appear to be independent of general taxonomic affinities. Both low and high concentrations of Ca appear within _Oribatei_ _inferiores_ and _superiores_. The low Ca concentration found in immature oribatids requires confirmation by additional measurements.

Intake rates. Nutrient intake is the product of concentration in food times amount of food ingested. Both of these are poorly known. Luxton (1972) concluded that the majority of oribatids are indiscriminate feeders (panphytophages) on a variety of fungi and decomposing vegetation. Fungus appears to be the preferred food for many oribatids and some exhibit selectivity in laboratory cultures. Mitchell and Parkinson (1976) found discrepancies between laboratory studies of food preference and gut analysis of field-collected specimens.

Nutrient content of food materials also varies greatly. For hardwood forest floors, raw litter contains about 10,000 ppm Ca and 5,000 ppm K. Leaching and decomposition remove K much more rapidly than Ca (Cromack and Monk 1975). Fungal hyphae evidently concentrate these elements. Rhizomorphs were shown to concentrate Ca and K 2 to 3 times higher than

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TABLE 1. Concentrations of mineral nutrients in individual cryptozoans, measured with microprobe methods.

Taxon	Ca Concentration (ppm)	K Concentration (ppm)
Pseudoscorpionida		
thorax	1600	4700
abdomen	850	5500
Cryptostigmata		
Liacarus	64300	2000
Liacarus	66100	2000
Liacarus	71300	2000
Camisia	10000	2500
Camisia	6100	2600
Cepheidae	56700	2800
Cepheidae	45500	2600
Hermannia	35000	900
Hermannia	28300	1100
Hermanniella	32200	1000
Tectocepheus	37300	800
Scheloribates	7400	1200
Phthiracaroidea	33500	400
immature	3900	1700
Prostigmata		
Bdellidae	400	1700
Rhagidia	300	3300
Pachygnathidae	300	2800
Mesostigmata		
Podocinidae	700	5600
Macrochelidae	500	1000
immature	1100	2000

in substrates (Cromack, Todd and Monk 1975). Little is known of elemental variation between fungal species, or through time.

Oribatid ingestion rates have been estimated for several species. Estimates range from 1% to 10% of body weight per day, with two exceptional higher cases (Mitchell and Parkinson 1976). Immature stages feed more rapidly than do adults, and seasonal differences occur as well as temperature responses.

Assimilation of nutrients. Some fraction of the ingested nutrients becomes "assimilated", that is, moves from the gut contents into the body tissues. Radioactive tracer methods provide the best available means for estimating this assimilated fraction. If cryptozoans are given a brief exposure to radioactive food, and then counted for radioactivity through time, radioactivity will decrease due to loss of tracer by defecation and excretion (it is assumed that appropriate corrections are made for radioactive decay). A graph of log radioactivity versus time reveals two components: rapid and slow. Experimentation (Van Hook and Crossley 1969) demonstrated that the rapid rate represents loss of nonassimilated tracer from the gut, while the slower rate measures excretion of assimilated tracer. Extrapolating the line for the slower rate back to the origin identifies the function of ingestion moving at that slower rate, and thus measures the fraction of tracer actually assimilated.

Different nutrients are assimilated at different rates, a point not always appreciated. Some authors have assumed that nutrient and energy assimilation are identical, which is erroneous.

Assimilation is overestimated unless exposure to radioactive tracer is kept brief. Highly radioactive food sources must be used to yield measurable levels of radioactivity in small cryptozoans following a short period of feeding. Luxton (1972) estimated ^{32}P assimilation by *Damaeus clavipes* to be about 60%. Gist and Crossley (1975*b*) reported even higher assimilation fractions for ^{85}Sr and ^{134}Cs. These authors evidently overestimated elemental assimilation due to prolonged feeding times in experiments. Crossley (unpublished) measured ^{85}Sr assimilation fraction by the collembolan *Sinella curviseta*. Measurements made after a one hour exposure to radioactive food gave an assimilation fraction of 29%. When exposure time was increased to 24 hours, the slowly-moving pool was estimated to be 80% of the body burden.

Goldstein and Elwood (1971) provided an alternative model which viewed assimilation as a rate, rather than a fraction. Although this is an attractive alternative, measuring the assimilation rate in their model requires that the assimilated pool be identified by curve-fitting, as described above. It might be hypothesized that assimilation fraction is an inverse function of temperature, or that it varies with previous nutritional condition. Neither of these effects has yet been demonstrated for cryptozoans.

Gut residence time, like assimilation, can be interpreted in different ways. One method is to observe the time from formation of a food bolus until its loss by defecation. This method assumes that material moves at a constant rate through the digestive system. Radioactive tracer experiments suggest that nutrients become mixed in the digestive system, and a constant fraction is then lost during defecation -- a first order model of the form:

$$\frac{dX}{dt} = -kX$$

where: X = unassimilated nutrient in the gut
k = gut turnover time

Data illustrated by Luxton (1972) for ^{32}P loss by Damaeus clavipes show such a relationship.

Excretion of nutrients. The turnover of assimilated nutrients can be measured with radioactive tracers of the nutrients or their metabolic analogs (Gist and Crossley 1975b). These rates are probably intrinsic physiological attributes of each species for the nutrients involved. They appear to be simple Q_{10} functions of temperature, at least within normal bounds. The slope of the longer component measured in radiotracer retention experiments is an adequate estimate of turnover rate.

Some workers (Kowal 1969, Kowal and Crossley 1971, McBrayer and Reichle 1971) have estimated turnover rates from radioisotope accumulation experiments rather than from retention experiments. Generally these methods are not as satisfactory because they do not yield any estimate of assimilation efficiency.

Summary. The values of parameters for a generalized input-output model for oribatids are summarized in Table 2. Ranges for values are large for most of the parameters. Consequently, a variety of different assumptions (low or high feeding or assimilation, slow or rapid turnover) can be made to yield the observed body contents of nutrients, and still be within the range of values reported. Additional experimentation will be required to evaluate the nutrient accumulation strategies for oribatid mites. Losses due to mortalities or changes in pool size due to migrations are not included (Gist and Crossley 1975c).

DIRECT AND INDIRECT ROLES OF ORIBATIDS IN NUTRIENT CYCLING

Soil fauna participate in mineral nutrient movement by ingestion, a mode which can be designated as "direct." By contrast, indirect effects of the fauna would be those influences on mineral nutrient movement which are not due to ingestion. For oribatid mites, information is not yet adequate for a confident evaluation of their direct participation in nutrient movement (Table 2). Estimates based on energy flow (e.g. Engelmann 1961) indicate that the direct contribution of oribatids to energy loss in decomposition is vanishingly small. A more significant direct role was found for oribatids in calcium cycling in a hardwood forest floor (Gist and Crossley 1975c), and for potassium in a white pine stand (Cornaby, Gist and Crossley 1975). Thus it seems premature to dismiss direct feeding as insignificant to nutrient cycling.

Estimates of the indirect effects of oribatids and other fauna on nutrient cycling have been largely speculative. Some field experimentation (e.g. Witkamp and Crossley 1966) and microcosm approaches (Patten and Witkamp 1967) have offered evidence that fauna can regulate aspects of nutrient cycling. Current developments are leading towards more complex conceptual models of nutrient mobilization in decomposition. Such models can be biologically more realistic in that they contain feedback loops rather than unidirectional flows or networks (e.g. Gist and Crossley 1975c). These models suggest that the distinction between direct and indirect participation by fauna may not be significant.

TABLE 2. Summary of parameters for Generalized Input-Output model for mineral nutrients in oribatid mites.

Parameter	Estimate	Reference
Intake:		
Food	1-10% body wt. per day	Mitchell and Parkinson 1976
Nutrient concentration in food	10,000-30,000 ppm Ca 5,000-20,000 ppm K	Cromack 1975; Cromack, Todd and Monk 1975
Assimilation:		
Nutrients	K(^{134}Cs): 80-100% Ca(^{85}Sr): 80-100%	Gist and Crossley 1975c
Turnover (19-20° C):	K(^{134}Cs): .04 per day Ca(^{85}Sr): .23 per day	Gist and Crossley 1975c
	K(^{137}Cs): .1-.4 per day	McBrayer and Reichle 1971
	Ca: .05 per day	Kowal 1969
Body Contents:	K: 1,000-3,000 ppm	This report
	K: 5,600 ppm	Gist and Crossley 1975a
	Ca: 10,000-60,000 ppm	This report
	Ca: 35,000 ppm	Gist and Crossley 1975a
	Ca: 60,000 ppm	Cornaby 1973

FIGURE 1. Compartment model of material transport through soil decomposition systems. Physical and biological processes are separated. Fauna act as catalysts in degradation of organic materials and enhanced microbial activities. Several feedback loops are illustrated.

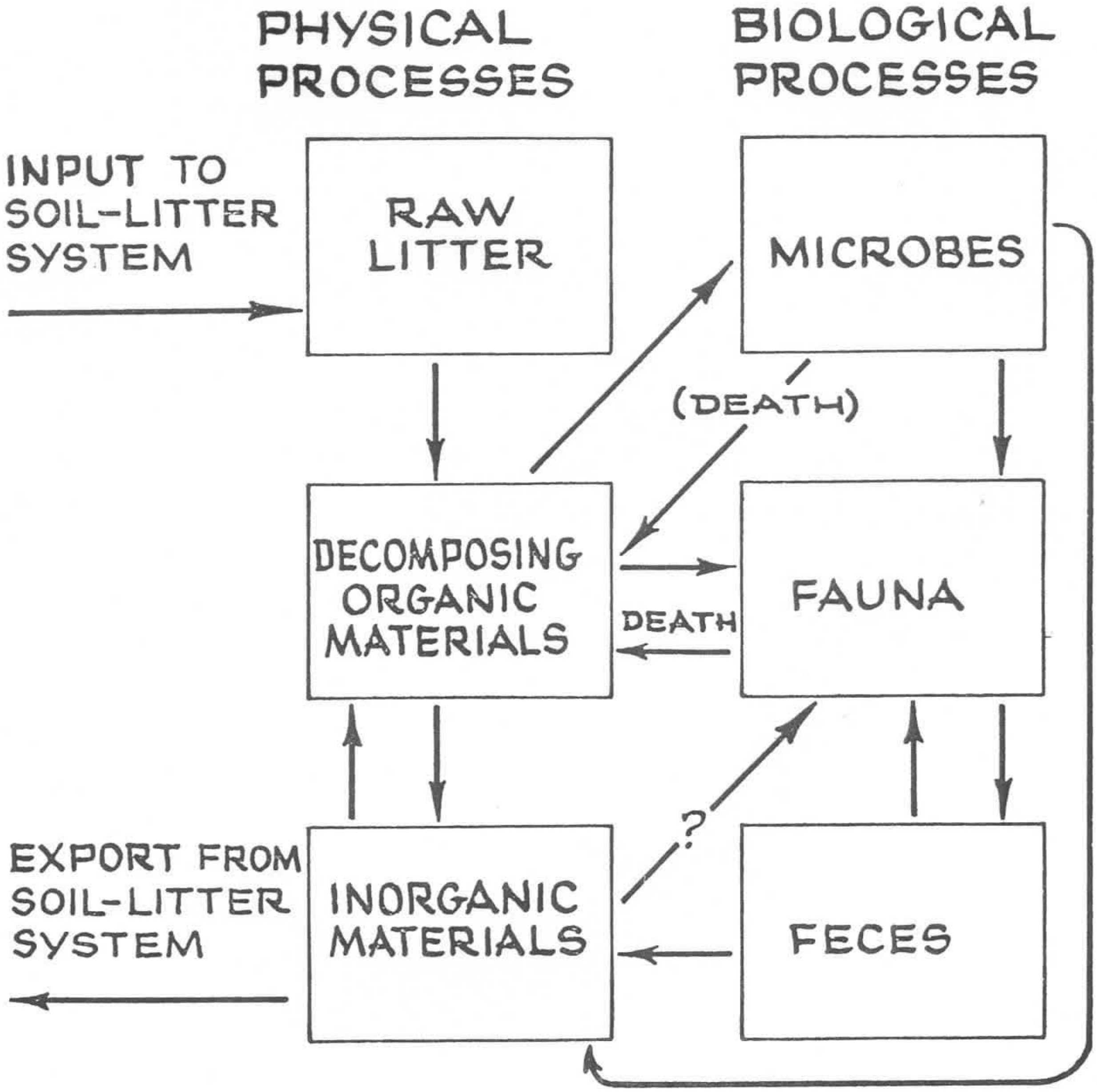

Figure 1 illustrates a conceptual model integrating soil fauna into the pattern of mineral nutrient flow. For conceptual purposes, physical and biological processes are separated. The degradation of raw litter to decomposing organic material is viewed as a primarily physical process of weathering. Once degraded to the point that biological processes become important, the organic debris may continue to lose nutrients by weathering, but losses are influenced by microflora and fauna (directly and indirectly). Feedback loops are illustrated between microflora and decaying substrate, as well as fauna and substrate. Multicompartmental loops are shown, including both biota and inorganic materials. The importance of some pathways and components doubtless varies between types of communities, and seasonally. For readily leachable nutrients (K) physical processes are assumed to be more important than for less leachable ones (Ca). The complex of loops in Figure 1 is assumed to regulate the general export from the system (to plant uptake or to other outputs).

The significance of some of the feedback loops in Figure 1 is the subject of current experimentation. Webb (in preparation) is evaluating the importance of arthropod feces as a nutrient pool, and the significance of the re-ingestion loop. Other research (Cromack, Sollins, Todd and Fogel 1976) is examining the importance of calcium oxalate production by fungi, its decomposition by bacteria, and the possible role of soil fauna in this aspect of Ca cycling.

It appears that current research is opening new avenues for exploring the roles of oribatids in decomposer systems. New methods of microanalysis, refined radiotracer techniques, soil biochemical approaches, and detailed conceptual models should yield a much improved insight into the importance of the millions of oribatids in the forest floor.

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